NOTES ON THE REVERSAL OF ASYMMETRY IN THE REGENERATION OF THE CHELÆ IN ALPHEUS HETEROCHELIS.

EDMUND B. WILSON.

We owe to Przibram[1] the interesting discovery that when the larger chela in the genus *Alpheus* (*A. dentipes*, *A. platyrrhynchus*, *A. ruber*) is removed, the chelæ undergo a reversal during the ensuing regeneration, a small chela being regenerated from the stump of the large one, while the former small chela, *which has not been injured*, is directly transformed at the first or second moult into a large one that shows the characteristic structural features of this appendage. A precisely analogous result was obtained in the annelids by Zeleny,[2] who found that after amputation of the functional operculum in *Hydroides* a rudimentary operculum was regenerated in its place, while the rudimentary operculum previously present on the opposite (uninjured) side developed directly into a functional one.

These cases are highly interesting since the reversal of asymmetry involves not merely the enlargement of a smaller structure on the uninjured side, but also profound structural and functional changes due to an injury to another part of the body.

During the summer of 1902 I had an opportunity at Beaufort, N. C.,[2] to repeat Przibram's experiments on *Alpheus heterochelis*, a form in which the differentiation between the two chelæ is extremely marked, and to make some observations on the control of the regenerative process by the nervous system. The anatomy, habits and development of this form have been carefully described by Brooks and Herrick,[3] whose observations give data having an important bearing on the facts to be described.

[1] "Experimentelle Studien über Regeneration," *Arch. für Entwkm.*, XI., 1901.

[2] "A Case of Compensatory Regeneration in the Regeneration of *Hydroides dianthus*," *Arch. für Entwkm.*, XIII., 4, 1902.

[3] I am indebted to the Hon. G. M. Bowers, United States Commissioner of Fisheries, for the privilege of occupying a table at the Beaufort Laboratory, and to Dr. Caswell Grave, director of the laboratory, for his kind coöperation.

[4] "The Embryology and Metamorphosis of the Macroura," *Mem. Nat. Acad. Sci.*, V., 4.

As shown in Fig. 1, *A*, *B*, the chelæ in this species differ very widely both in size and structure; right-handed and left-handed individuals occur in approximately equal numbers. The large or hammer chela (*B*), which is nearly or quite half the length of the whole animal exclusive of the antenna, is greatly swollen, with a deep transverse groove on either side of the propodus, and a characteristic color-pattern. Both claws are extremely stout, and show very remarkable and characteristic features. On the concave side of the dactylus is a great swollen knob, forming the "hammer" (*h*), which fits into a corresponding deep socket on the outer side of the propodus claw, overhung on the upper side by a prominent setose ridge (*p. s.*). By fully extending the dactylus and then suddenly snapping the claws together the hammer is forced into the socket with such force as to produce a surprisingly loud report, whence the popular name "pistol crab" applied to the animal in some localities (*cf.* Brooks and Herrick).

The large chela has essentially the same structure in both sexes, but the small one shows characteristic sexual differences. In the female (Fig. 2, *D*) it is very straight and slender, and relatively smaller than in the male. In the latter (Fig. 2, *A*) it is not only relatively somewhat larger, but stouter, with relatively shorter claws, the dactylus more strongly curved, and traces of the transverse grooves of the large chela are often present (Fig. 1, *A*). Its most characteristic feature in the male is the presence on both sides of the dactylus of a very marked curved ridge, bearing a series of stiff, short setæ (*d. s.*). A somewhat similar but straighter setose ridge (*p. s.*) is also present on each side of the propodus claw in a position corresponding to that of the setose ridge in the large claw. No trace of the hammer is present in either sex. Ordinarily the small chela alone is used in taking food, the large one being in the main a weapon of offense and defense, as Brooks has graphically described.

As far as the reversal of asymmetry is concerned my observations on *A. heterochelis* entirely confirm those of Przibram on the three species studied by him, but give a slightly different result in cases where both chelæ are amputated. Przibram found (*op. cit.*, p. 331) that in such cases each stump regenerates an appendage of the same type as that which has been removed (*i. e.*, no

reversal occurs) but the two are of nearly equal size. The species I have studied agrees in showing no reversal after this operation, but the hammer claw is from the first in most cases very distinctly larger than the other; though as was to be ex-

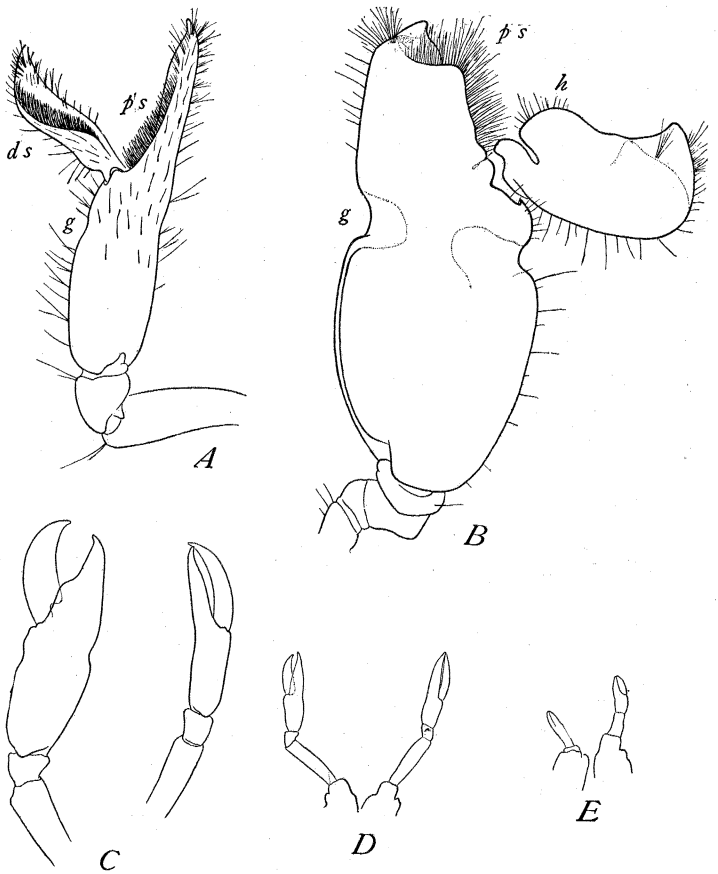

FIG. 1. Normal and regenerating chelæ of *Alpheus heterochelis*, × 4.

A, *B*. Left and right chelæ of male; *d. s.*, setose ridge of dactylus, *p. s.*, setose ridge of propodus; *h*, hammer; *g*, transverse groove, only faintly indicated in the small chela.

C. Chelæ regenerating without reversal, after removal of both appendages from a left-handed specimen; immediately after first moult, twelve days after operation.

D. Chelæ of originally left-handed individual, regenerating very slowly without reversal after removal of both chelæ; eleven days after operation.

E. Regenerating chelæ of originally left-handed individual, three days after removal of both chelæ. Differences of the chelæ already apparent; no reversal (the appendages are viewed from the lower side and hence appear reversed as compared with the other figures).

pected the unequality is very much less marked than in a normal specimen (Fig. 1, *C*, *D*, *E*). A comparison of Przibram's Figs. 20–23 (*A. dentipes*), 32–35 (*A. platyrrhynchus*) with mine shows that in point of fact the difference is one of degree only; for in both those species also the figures represent the hammer-claw as slightly larger. The most important addition I am able to make to Przibram's result is the fact that if, after removal of the large chelæ, the nerve of the remaining small chela be cut at the base, *the reversal in some cases at least does not take place, or is incomplete.*

In all, more than a hundred operations were performed, but owing to the large mortality to be expected under the conditions given by the lack of running water in a warm climate not more than half gave definite results, and I shall here report only on such cases.[1]

A first series, including a simple repetition of Przibram's work, gave the following result:

First Series.

A. Of 17 cases in which the large chela was removed, all without exception regenerated in the reversed condition, the remaining small chela being transformed into one of the large type.

B. Of 15 cases in which both chelæ were removed 14 regenerated without reversal — *i. e.*, large and small chelæ reappeared on the same respective sides as before the operation — while a single specimen regenerated reversed.

In three of the cases under *A* the larger chela (originally the smaller) formed on the uninjured side was removed soon after the moult, with the result that a second reversal took place, restoring the original condition. One of these cases is illustrated by Fig. 3, *A–C*. The animal, a female, had originally the

[1] The animals were kept singly in bowls, the water being changed once or twice daily, and were abundantly fed on oysters, which were greedily devoured. A complete permanent record of the experiments was kept by preserving every cast skin and the animal that emerged from it, so that there can be no doubt as to the condition of the animal before and after the moult. As a rule the animals were fixed soon after the first moult; but in cases where it occurred soon after the operation they were kept until the second moult. The moults occurred at intervals of 9 to 14 days.

large chela on the left side. The first moult occurred nine days after removal of the large chela; Fig. 3, *A*, shows the cast skin of the original small (right) chela, *B*, the same appendage removed three days after the moult, showing the characteristic features of the large chela (transverse groove, shortened and thickened chela, and the "hammer"). The second moult occurred six days later (nine days after the first moult); Fig. 3, *C*, shows the result, the appendage having returned to its original condition, except in size, while a chela of the large type had appeared on the other side.

In all cases the hammer-chela on its emergence from the skin of the small chela is less modified than that of a normal animal, always showing characters intermediate between those of the fully developed hammer-chela and the small chela; and the same is true of the regenerating hammer-chela after both chelæ have been removed. In general the longer the period between the operation and the ensuing moult the greater the modification of the hammer-chela. As may be seen from the figures the reformed or regenerating hammer-chela is less robust than the fully developed one, the claws are longer and less curved, the transverse groove less pronounced and the setose ridge of the propodus (*p. s.*) further removed from the tip of the claw. All these characters become more and more accentuated as the period between operation and moult increases. The shortest observed period in which the regenerating chelæ (after removal of both) showed distinct differences was three days (Fig. 1, *E*); but the difference is here still one of size and general development only. After removal of the large chela only the structural differences may become clearly apparent after five days, as shown in Fig. 2, *G*, *H* (though in this case the remodelled small chela fixed nine days after the moult has probably undergone some further change). In this interesting case the hammer-claw very clearly shows a combination of characteristic characters of the small and large chelæ. It still retains on the whole the general proportions of the small chela of the male, but is more robust, the claws are somewhat shorter, the transverse groove has appeared, and the "hammer" has begun to form. The most interesting point is the retention of the characteristic setose ridge (*d. s.*) of

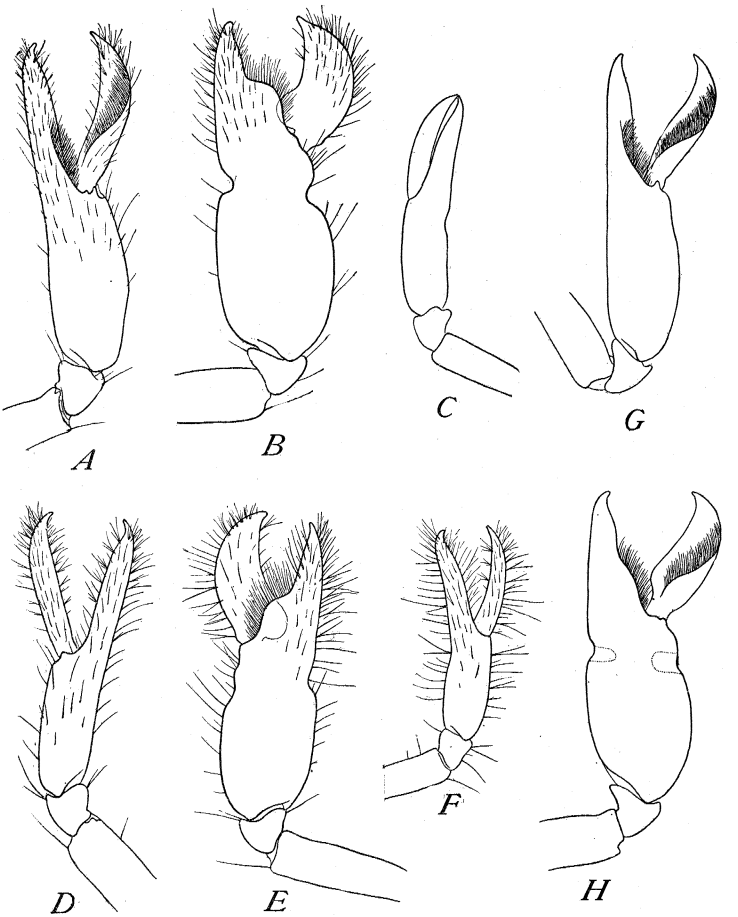

FIG. 2. Typical reversal, after removal of large chela, ×4.

A, *B*, *C*. Reversal in a male, originally left-handed ; result of first moult, eleven days after removal of large chela. *A*. Cast skin of original small right chela. *B*. Right chela immediately after moult, showing transformation into hammer-chela well advanced. *C*. Left chela, immediately after moult, regenerated on the stump of the large chela removed.

D, *E*, *F*. Reversal in a female slightly larger than the specimen shown in *A–C*, originally right-handed ; result of first moult, sixteen days after removal of large chela. *D*. Cast skin of original small left chela. *E*. Left chela immediately after moult, transformation less advanced than in the male. *F*. Right chela, immediately after moult, regenerated on the stump of the large chela removed.

G, *H*. Initial changes in the typical reversal of an originally left-handed male. *G*. Cast skin of right chela, after first moult, five days after removal of the large left chela. *H*. The same appendage nine days after the moult, showing remodelling in progress, but still retaining the setose ridge on the dactylus.

the dactylus of the male small chela, which is entirely absent in the more modified forms (*e. g.*, in Fig. 2, *B*, *E*). A comparison of the figures will show that in every respect the specimen is intermediate between the unmodified male small chela (Fig. 2, *A*) and the more modified form (Fig. 2, *B*). In specimens of 9 days the setose ridge of the dactylus has wholly disappeared (Fig. 3, *B*) and, except for its somewhat more slender form, is as characteristic as in those of two weeks or more (Fig. 2, *E*).

Second Series.

In a second series the same operations were performed, but in addition the nerve supplying one or both stumps was cut below the base of the appendage. In one set (*C*) the large chela was removed and the nerve of the remaining small chela on the opposite side was cut; in a second set both chelæ were removed and the nerves of both stumps cut. This operation, easily performed by means of a slender sharp-pointed scalpel, results in the first case in a complete paralysis of the remaining appendage. If after a few days control of the appendage was regained, as often happened before the ensuing moult, the operation was as a rule repeated. The mortality in operations of this type is large, and many of the specimens sooner or later cast the remaining appendage; hence only eight successful cases were obtained, and of these only two are beyond question.

C. Of eleven cases in which the large chela was removed and the nerve of the remaining small chela was cut, nine regenerated without reversal, one with reversal, and one with both chelæ of the large type.

D. Of three cases in which both chelæ were removed and the nerves of both stumps cut, all regenerated without reversal. These cases differed from those recorded under *B* only in showing a slight retardation in regeneration.

Of the first nine cases recorded under *C* seven had thrown off the small claw at a varying period before the moult and hence are without value; for such specimens have lost both chelæ. Experiments to test this point show in fact that if the large chela be removed and the smaller one be subsequently removed, after a period sufficiently long to admit of complete reversal under

ordinary conditions, the animal regenerates without reversal. For example, from a male left-handed individual the large chela was removed and twelve days later (a period long enough to effect a complete reversal, as shown by other experiments) the remaining small chela was also removed. The animal moulted nine days later (twenty-one days after the first operation) and is *not reversed* showing a typical small chela on the right side and a large one on the left, which however is less modified than usual.

The absence of reversal in the seven cases in which the remaining chela was cast may have been due to the same cause as in the above experiment; but two cases remain, that seem beyond question, though one of these did not moult quite normally and the other not at all. The first case (Fig. 3, *D–F*), a right-handed male, moulted nine days after the operation, but did not succeed in extricating the small chela from the cast skin. The appendage was, however, easily drawn out by hand, in an apparently quite healthy condition, and fixed in formalin. From the right stump of the large chela had been regenerated one of the same type (Fig. 3, *F*), which though still small, shows clearly enough all the characteristic features of the appendage. The appendage drawn out of the cast (Fig. 3, *E*) is on the whole of the small type but has lost the characteristic setose ridge of the dactylus, and shows an indication of the hammer. It is, however, far less modified than the uninjured appendage after the same period of time (Fig. 3, *B*).

The second case, which did not moult, is shown in Fig. 3, *G*, *H*, fourteen days after the operation. The appendage developed on the stump of the large chela, though small, is plainly of the large type. The small (left) chela, owing to the absence of a moult, shows no change.

The foregoing data are too meager to have a very high value, yet they render it probable that the moulding of the small chela into one of the large type, and the production of the small one on the opposite side is controlled by the nervous system — a result in accord with Herbst's remarkable observations on the regeneration of the eye in *Palæmon* and Morgan's on the regeneration of the head in *Allolobophora*. It is possible that the failure of reversal in such operations in *Alpheus* is due to a circu-

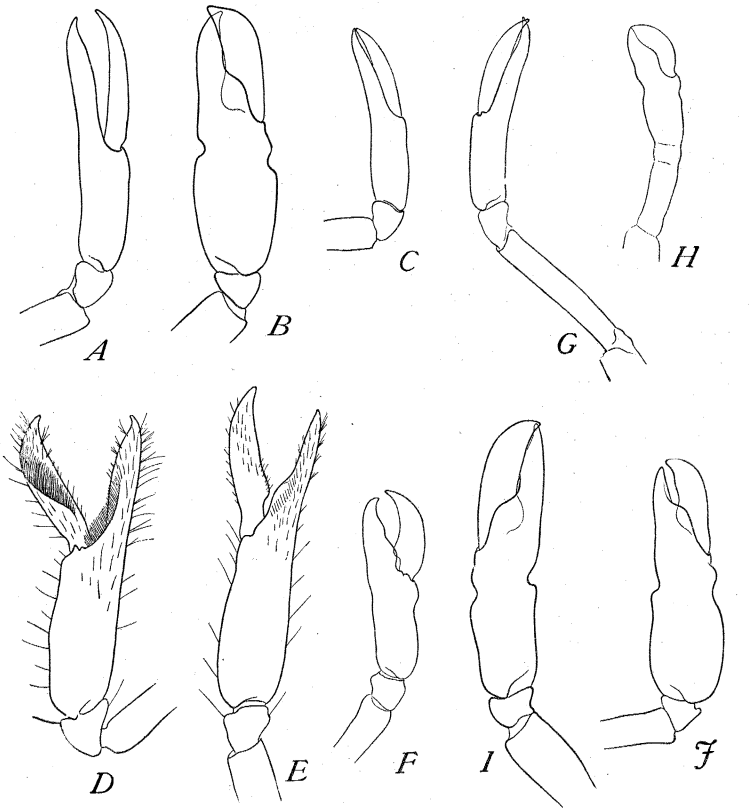

FIG. 3. Normal reversal, and partial inhibition of the reversal after section of nerve of small chela, ×4.

A, *B*, *C*. Double reversal after two successive amputations of large chela. *A*. Cast skin of right chela, female, first moult, nine days after removal of left large chela. *B*. The same appendage amputated three days after moult. *C*. Appendage regenerated on the same stump, immediately after the second moult, six days later; restoration of the original condition. The left chela is again of the large type.

D, *E*, *F*. Partial inhibition of reversal by section of the nerve of the small chela after removal of the large one; originally right-handed male. *D*. Cast skin of small chela at moult, nine days after operation. *E*. The same appendage withdrawn from the cast at the moult. *F*. The right chela, showing distinct features of the large type.

G, *H*. Partial inhibition of reversal after section of nerve. Originally a right-handed female. *G*. The small chela, fourteen days after operation; no moult. *H*. Chela of large type regenerating on stump of large chela removed.

I, *J*. Formation of chelæ transitional to large type on both sides after amputation of large (right) chela and section of nerve of remaining small chela. Originally a right-handed female. Appendages as they appeared after the first moult, fourteen days after operation. Two days before the moult the left chela showed a regain of nervous control.

latory or other non-nervous disturbance. Since, however, the appendage remains in a healthy state and emerges from the moult in a quite normal condition and without sign of atrophy, it seems more probable that the effect is directly due to the lack of nervous control.

The two exceptions recorded above are of considerable interest. In the first case the animal, originally a right-handed female, shows a perfectly typical reversed condition. In the second, the animal, originally a right-handed female, has regenerated both chelæ of the large type, showing the characteristic hammer and other distinctive characters (Fig. 3, *I*, *J*). The left chela (originally the small one) is, however, distinctly less modified than the right, being more slender, with longer and more slender claws, and is in this and other respects clearly intermediate in character between chelæ of the large and small type (Fig. 3, *I*). *Both these specimens, and these alone of those recorded, had regained partial control of the remaining appendage before the moult.* Unfortunately the record does not show precisely how long the control had been regained before the moult. The facts indicate, however, that in the first case the nervous connections had been reëstablished relatively early, so that the typical metamorphosis took place. This case probably gives an interpretation of the second one, which may be explained by supposing that in the early period, before the nervous connections were established, the stump of the large chela (right) had already partially regenerated a chela of the same type (as in the typical case); but that the transformation did not proceed so far as wholly to check the metamorphosis of the small chela (left) upon the reëstablishment of control. Both claws, therefore, reappeared of the large type, that on the right, however, being more modified than the other.

Reversal in Relation to the Secondary Sexual Characters.

The experiments bring out some interesting points in relation to the secondary sexual characters (which were not studied by Przibram) and offered data of some importance for the general interpretation of the facts. These concern especially the

structure of the small chela, which differs widely in the two sexes.[1]

In the female *Alpheus* this appendage is distinctly less modified than in the male (Fig. 2, *D*), being of slender form, with the claws straighter, weaker and longer. In the male (Fig. 2, *A*), the chela is of more robust form, the dactylus is more curved, and bears on each side a prominent curved ridge armed with a close series of strong setæ, while the fixed claw of the propodite has on each side a similar but straighter and weaker ridge also covered with setæ. Both these ridges are absent in the female. A comparison of Figs. 1, *A*, *B*, 2, *A*, *D*, clearly shows that in some of these respects the small chela of the male is intermediate in type between that of the female and the large chela, which is essentially of the same type in both sexes. This appears in the robuster form of the male chela, the occasional presence of a slight transverse groove on the propodus corresponding to the deep groove on the large chela, the greater thickness and curvature of the dactylus, and the much greater prominence of the seta-bearing ridge on the claw of the propodus, which obviously corresponds to the prominent setose ridge in the corresponding position on the large chela. The female small chela is obviously of more generalized type; and as far as can be judged from the figures of Brooks and Herrick is closely similar to both chelæ of the larval form, on their first appearance.

With these points in mind it is interesting to compare the chelæ of an animal after the first moult subsequent to removal of the large chela. *In both sexes the small chela, regenerated from the stump of the large one, is of the female type* (cf. Figs. 2, *D*, *C*, *F*) *while in both the re-forming large chela is intermediate in form between the fully developed* large chela and the small chela of the male. Furthermore, a comparison of the large chela, in regenerated individuals, shows in general that the longer the period after the operation, the greater its divergence from the small chela. Consideration of the sexual differences brings out the further interesting fact that the transformed small chela of the male for the same period of time is more highly modified than that of the female. This is clearly shown by a comparison of

[1] *Cf.* Coutière, "Les Alpheidæ," *Ann. Sci. Nat. Zoöl.*, VIII., 9, 1899.

Figs. 2, *B*, 2, *E*. The former shows the transformed small chela of the male, the latter that of the female. The former is in every respect — general proportions, depth of transverse groove, shape and proportion of the claws — more highly modified in the direction of the adult hammer-chela, though the period since the operation was eleven days, while in case of the female it was sixteen.

These facts seem to leave no doubt that the female small chela represents a relatively undeveloped or larval type, that of the male a further development of the same type, accompanied by the appearance of certain specialized secondary sexual features (setose ridge), while the large chela is the extreme of the same line of development. The male small chela is more rapidly transformed into one of the large type, common to both sexes, because it has already advanced further on this line than that of the female.

Comment.

In the above facts we probably find a basis for an interpretation of the reversal of asymmetry during regeneration. The great size of the large chela in *Alpheus*, and its importance as a weapon of offense and defense which Brooks and Herrick pointed out, suggest at once the teleological interpretation that the reversal is a device to secure the least possible delay in the restoration of an important organ by utilizing a structure already present as the foundation of the large chela. That this result is actually effected by the reversal is beyond question; but we need not for this reason assume that the reversal has been specially acquired for this purpose. Structurally the small chela of the female represents a large chela in a state of arrested development, with hardly noticeable modifications of the larval type.[1] That of the male represents a slightly more advanced development along the same line, together with certain special modifications — notably the setose ridge upon the dactylus. In both sexes, accordingly, its transformation into a hammer-chela repre-

[1] The figures of Brooks and Herrick (*op. cit.*, Plate XX., Figs. 2, 3) of the larval form of this species are not sufficiently detailed to prove this completely, but show both chelæ of equal size and, as far as can be judged, nearly similar in form to the adult female small chela, or the regenerating small chela of both sexes.

sents, in its main features, the completion of a process that is inhibited or held in abeyance in the normal condition; though in the male this forward movement is accompanied by a regressive process which causes the disappearanee of its specific modifications (setose ridge of the dactylus). To vary the statement, the development of *Alpheus*, at first symmetrical, tends towards a state of equilibrium, characteristic of the species, which is attained through a great inequality in the size of the two chelæ and a series of structural modifications affecting especially the larger one. With the removal of the larger chela the normal equilibrium is reversed and the restorative process proceeds on both sides along the same general lines as in the normal development until a condition of normal equilibrium is restored. A similar interpretation will perhaps apply to Brachyura examined in Przibram's second interesting communication,[1] where it is shown that after the removal of either or both chelæ the regenerated form is always that of the less modified form (which is usually also the smaller). Where only the crushing chela is removed the remaining chela is not transformed into one of the other type; hence no reversal occurs. This case is clearly intermediate between that of *Alpheus*, in which complete reversal occurs, and *Homarus*, in which, as Przibram shows, no reversal occurs, each chela regenerating one of its own type whether one or both is removed. The Brachyura in question (*Carcinus*, *Portunus*, *Eriphia*) exhibit one element of the reversal, namely, the formation of a less modified chela from the stump of the crushing-chela; but fail to complete the metamorphosis of the remaining one. This may be due either to the slowness of the process (which may require a longer time for its completion than that during which the animals were kept under observation) or to a greater rigidity of organization. In *Homarus* the regenerating crushing claw is not in its very early stages recognizable as such, but is of the embryonic type; it assumes many of its characteristic features very early, but for a long period remains of a type intermediate between the two forms of chelæ (*cf.* Przibram's Figs. 13, 14). No reversal occurs. These various cases

[1] "Experimentelle Studien über Regeneration," II.; *Arch. Entwkm.*, XIII., 1901–02.

obviously form a series, at one extreme of which the large chela, after its removal, reappears and remains permanently of the small type, with transformation of the small chela into one of the large type (*Alpheus*); in the Brachyura the first process occurs but not (as far as the observations show) the second; while in *Homarus* the large chela shows transitional characters from a very early period.

In the case of *Alpheus* it is a tempting conclusion that the initial factor (*Auslösung*) that sets in motion the complex process of differentiation of which either side is capable, is primarily only a difference in the amount of material on the two sides.

Mr. C. T. Brues has at my suggestion undertaken a study of the internal changes and has determined the interesting and unexpected fact that the nerves supplying the two chelæ do not differ perceptibly in size; and they appear further not to differ in the number of the component nerve-fibers or the size of the ganglionic centers from which they proceed. As far as the nervous system is concerned, therefore, the adult appears to retain the bilateral symmetry of the larval form, the asymmetry arising through hypertrophy in other tissues, Removal of the large chela obviously reverses the asymmetry in respect to these tissues, and must temporarily at least, lead to a functional nervous difference on the two sides which may be accountable for the release of development in the small chela. This is, however, only a suggestion that must await further test.

The interest of the general interpretation offered above, which is essentially similar to the one suggested by Zeleny in the case of *Hydroides*, seems to me to lie in the explanation that it offers, of a regulative process of undoubtedly high utility to the animal, that is in the main effected by the same factors as those operative in the normal development; and it seems not unlikely that many regulative processes in regeneration may be capable of a like interpretation.

ZOÖLOGICAL LABORATORY, COLUMBIA UNIVERSITY,
January 15, 1903.